Ship fouling: a review of an enduring worldwide vector of nonindigenous species

Final Report

Prepared for:

The California State Lands Commission

Marine Invasive Species Program

Prepared By:

Ian Davidson, Mark Sytsma, Greg Ruiz

Aquatic Bioinvasion Research & Policy Institute

A partnership between

Portland State University and the Smithsonian Environmental Research Center

November, 2009

Abstract

Ships have transported organisms deliberately and inadvertently for millennia, since the first vessels were launched, breaking down biogeographic barriers and altering the distributions of thousands of species. Ship biofouling, a long-time scourge of shippers, has been a dominant source of transfers for marine biota, including both sessile organisms and matrix-dwelling mobile species. Despite its relative importance as a historical and contemporary transfer mechanism (vector) of organisms, current understanding of the ship fouling vector laggs behind that of ballast water and other sources of marine invasions. The aim of this study was to provide a broad overview of the available literature on ship fouling, highlighting taxonomic and richness patterns of organisms on ships and identifying information gaps. We also examined eight well-studied temperate locations from around the world to characterize the influence of fouling on species introductions.

Our literature search revealed 36 papers and reports (grey literature) with direct sampling of ships' submerged surfaces that provided ecological data including lists of macro-fouling organisms. Studies of recreational boats were not included. An additional 90 papers that refer to ship fouling were identified in the search, many of which were concerned with antifouling paints and ecotoxicology, but did not provide original data regarding biofouling composition or extent from ships' hulls.

Although limited to a subset of vessel types and regions, data collected directly from ships' hulls highlighted the diversity of organisms associated with this vector. Across the 36 studies since 1910, a total of 1128 species from 21 phyla or divisions have been recorded. Twenty of the 36 studies used comparable methodology that allowed comparison of taxonomic composition, indicating that arthropods were most commonly recorded (33% of all species), followed by annelids, molluscs and bryozoans. Seventy-three different barnacle species have been recorded on ships and *Amphibalanus amphitrite* was the most commonly recorded among studies. A majority of species (77%) have been recorded in one study only. Although most vessels sampled in the literature

had fewer than 10 species on their submerged surfaces, richness of up to 115 species has been recorded.

The vector process (effect of transit) itself is poorly understood. Only 9 vessel voyages from 5 studies have documented changes in diversity and abundance by comparing measures on the same vessels for source and destination ports. These limited data indicate a highly variable response to environmental conditions of voyages, ranging from complete removal of biota to unexpected increases in species richness. The source of such variation and general conclusions about transit dynamics remains unresolved, until further data is available.

A larger volume of data exists to evaluate the effect of duration-since-dry-docking (age of antifouling paint) on biofouling accumulation. We evaluated such data from 163 vessels. In general, there was a positive relationship between richness of biofouling species and duration since dry-docking, but there is much variation (spread) in the data, and differences among studies (pre-1928 versus post-1996) were not discernable. There is not yet sufficient data available to statistically evaluate the separate effects of paint type, vessel speed, geographic location, and voyage route/history on biofouling accumulation.

Despite some of the current limitations, ship sampling studies to date have revealed that a high diversity of species are transferred regularly by ships, including modern faster ships, and many of the species are non-native to recipient ports simply because voyage ranges often traverse biogeographic barriers. For example, a study in Germany recorded 74 nonindigenous species (NIS) incursions (67% of the richness sampled) and more than one-third of the barnacles, bivalves, ascidians and bryozoans that have been sampled on ships have been designated as non-native to the sampling location.

To underscore the relative importance of hull fouling as a vector, we examined its relative contribution to established invasions at eight temperate global locations, where invasions have been well documented: Belgium, Germany and Ireland in Europe; Puget

Sound, San Francisco Bay and LA/Long Beach on the US West Coast; and New Zealand and Port Philip Bay (Melbourne, Australia) in the southern Hemisphere. A total of 838 records of 553 different NIS have been recorded across these sites including 102 algal species, 129 arthropods, 75 molluscs, and 56 bryozoans. The amphipod, *Caprella mutica*, and ascidian, *Styela clava*, are the most widespread species, both occurring in seven of the eight locations. A majority of NIS (72%) occur in one of the eight sites only. Ship fouling was a sole or possible vector for 73% of the 553 species. For some taxa, including ascidians and cnidarians, ship fouling has been widely assigned as the sole or primary vector causing NIS occurrences. San Francisco Bay, New Zealand and Port Philip Bay had the highest numbers of NIS, each with more than 150, while the other five locations had less than 80 each. Ship fouling was considered the primary vector (having transferred most NIS) at LA/Long Beach and both southern Hemisphere sites, mainly because high proportions of molluscs and arthropods at these sites were considered ship fouling incursions while at other sites these taxa were vectored by other means.

The importance of ship fouling on the biogeography and dispersal of many taxa may be underappreciated, especially as a contemporary vector that is still potent, partly due to the small number of studies with direct hull sampling. In an increasingly connected world, particularly the hub-and-spoke world of ports and ships, fouling of vessels continues to play a significant role in the re-making of species biogeographic distributions. Since 1990, fully two-thirds of NIS introductions at the eight locations examined were associated with biofouling of ships as a possible vector, whereas only one-third were considered unambiguously to have arrived via vectors other than ship fouling.

Most of the recent research on biofouling has been directed toward measures of propagule identity and quantity, both important components of risk. The documented species diversity associated with hulls begins to characterize species flux, but this is certainly an underestimate, given the limited scope of analyses to date that exclude many vessel types, geographic regions, and routes. However, conspicuously absent from current studies are analyses of propagule quality and the likelihood of colonization for biofouling organisms. In particular, the condition, viability, and reproductive status of biofouling organisms that arrive on ships' hulls have received little attention. These attributes are critical to understanding invasion risk, however, and have important implications for management that aims to reduce hull-mediated invasions. Thus, further analyses should strive to address gaps in knowledge associated with species performance (quality) as well as flux (arrival) for biofouling communities.

Introduction

The initial transfer phase of species introductions involves a complex step-wise process where vector and organism characteristics interact (Mack et al., 2000; Ruiz & Carlton, 2003). The most prominent vectors, therefore, are those that maximize: 1) frequency and geographic range of vector activity, with 2) abundance, diversity and survivorship of associated organisms. These criteria explain the major contribution of maritime shipping to nonindigenous species (NIS) transfers. Ships can transfer terrestrial species on-deck and in cargo while transporting a diversity of marine organisms in ballast water and on submerged external surfaces within the fouling community. No other vector is responsible for transferring as many marine species or individual organisms across biogeographic barriers, especially on such a global scale (Carlton, 1985; Carlton & Geller, 1993; Ruiz et al. 2000).

Several milestones throughout the millennia of maritime history have caused shifts in ship vector characteristics, affecting the types and rates of marine species transfers (examples of milestones are shown in Fig. 1 & 2). For example, the ship vector 'footprint' was minimal initially (>3000 years ago) because the earliest vessels were small and oar-powered, and voyages ranged over local and then regional scales. This remained the case for thousands of years until ship construction matched the seaworthiness required to traverse longer open-ocean distances. A notable early development occurred in Egypt where 75-foot-long complex vessels constructed using planks of wood bound together have been dated to 5000BP (Before Present)(Lloyd, 1975; Natkiel & Preston, 1986; Ward, 2006). The civilizations of the Mediterranean, including Crete, Phoenicia, Greece, and Rome, subsequently developed specialized ships for warfare and trade while maritime capacity also developed throughout the Middle East, India, China and Japan (Lloyd, 1975; Natkiel & Preston, 1986).

Voyage ranges increased as ship design developed, probably resulting in regional changes to species distributions (along the same coastline or within the same sea). Transoceanic and intercontinental maritime transits, however, were not reliably documented until the 15th century (Fig. 1; Mack et al., 2000). From 1400 to 1800, significant strides or milestones occurred in the development of sail and reliable navigation that extended the global reach of ships and altered the historical ranges of coastal species' on inter-continental scales. This time period (age of discovery and sail) is recognized as an important pulse of terrestrial (Mack et al., 2000; Hulme, 2009) and marine species introductions (Carlton & Hodder, 1995; Hewitt et al., 2004). Marine organism transfers occurred within solid ballast material used in ships for trim and stability, as well as within wooden hull fouling and boring communities. It had long been recorded that vessel hulls of the time (and prior) were compromised by ship boring and fouling pests (see Carlton & Hodder, 1995), including half of Columbus' expedition fleet in 1502 that was lost to infestation by the shipworm *Teredo* (Natkiel & Preston, 1986). The practice of unloading ships to float or beach a vessel on its side for cleaning, known as careening, was an early hull husbandry technique widely documented and famously illustrated by Sir Francis Drake on his visit to the Pacific Coast of North America (Holmes, 1969). As rudimentary antifouling technology developed to prevent pest species from slowing or destroying ships (Maurer, 1950; Carlton, 1985; Callow & Callow, 2002), the biogeographic consequences of transferring those species went largely unrecorded, complicating later efforts to differentiate natural and human-mediated ranges of many species (Carlton & Hodder, 1995; Carlton, 1996).

The ecological implications of ships as vectors of marine species, and more specifically ship fouling as a vector, were documented by Darwin in 1854 when he wrote in relation to barnacles that, "it should not be overlooked, that those species, which seem to range over nearly the whole world (excepting the colder seas), are species which are habitually attached to ships, and which could hardly fail to be widely transported" (Darwin, 1854). In the same monograph, Darwin also noted that some species commonly found on ships' hulls had quite restricted ranges. Further developments in vessel power (sail to steam to oil), vessel construction (wood to iron to welded steel), shipping practices (e.g. switch from solid to water ballast) and inter-oceanic canal construction throughout the 19th and the first half of the 20th century marked a period of great significance for ship-mediated species transfers (Fig. 2). Each of these milestones influenced the 'selection' of organisms by ships or the speed at which they were transferred. The speed of transfer can have the effect of reducing organism retention on ships' hulls, although higher speeds can also increase the likelihood of voyage survivorship because of shorter voyage durations (Minchin & Gollasch, 2003). The validity of ship fouling as a means of extending species distributions was questioned briefly (e.g. Visscher, 1938), but the vector was responsible for transferring marine species to new distant locations where self-sustaining populations had become established (Allen, 1953).

In modern times, the growth of maritime trade and increased global connectivity brought about a significant escalation in shipping traffic and voyage routes that have coincided with an exponential increase in the numbers of coastal nonindigenous species reported throughout the world (Ruiz et al., 2000; Hewitt et al 2004; Gollasch, 2006). Ship fouling is widely acknowledged as a historically significant vector of organisms. In addition, recent introductions point to the contemporary importance and enduring nature of the vector despite the effectiveness of modern antifouling paints (Nehring, 2001; Hewitt et al, 2009). Several authors have suggested that studies of ship fouling are limited in number and scope, however, and that contrary to ballast water research, a scarcity of biofouling studies with direct vessel sampling belies the vector's prevalence and significance (Godwin, 2003; Minchin & Gollasch, 2003; Drake & Lodge, 2007; Mineur et al., 2007).

In this report, we reviewed the ship fouling literature to summarize the state of knowledge about the magnitude and diversity of transfers of biofouling communities on ships. Specifically, the aims of this study were to evaluate: 1) the number, timing and geography of studies with original data collected from ships' hulls, 2) the taxonomic and richness patterns within and among studies, 3) the effect of voyages and hull husbandry on organism transfer, and 4) the prevalence of nonindigenous species within fouling communities. We also evaluated ship fouling vector strength – the number of established introduced species considered to have arrived via ship fouling (Ruiz & Carlton, 2003) – for eight well-studied locations around the world.

Figure 1. Historic milestones in maritime shipping and ship vector activity. A selection of milestones highlights the development of maritime shipping throughout history (prior to 1800). The influence of ships on organism dispersal through the oceans is summarized (right side column). Historical information is from Lloyd (1975), Karmon, 1980; Natkiel & Preston (1986), Ward (2006), and Galil (2008).

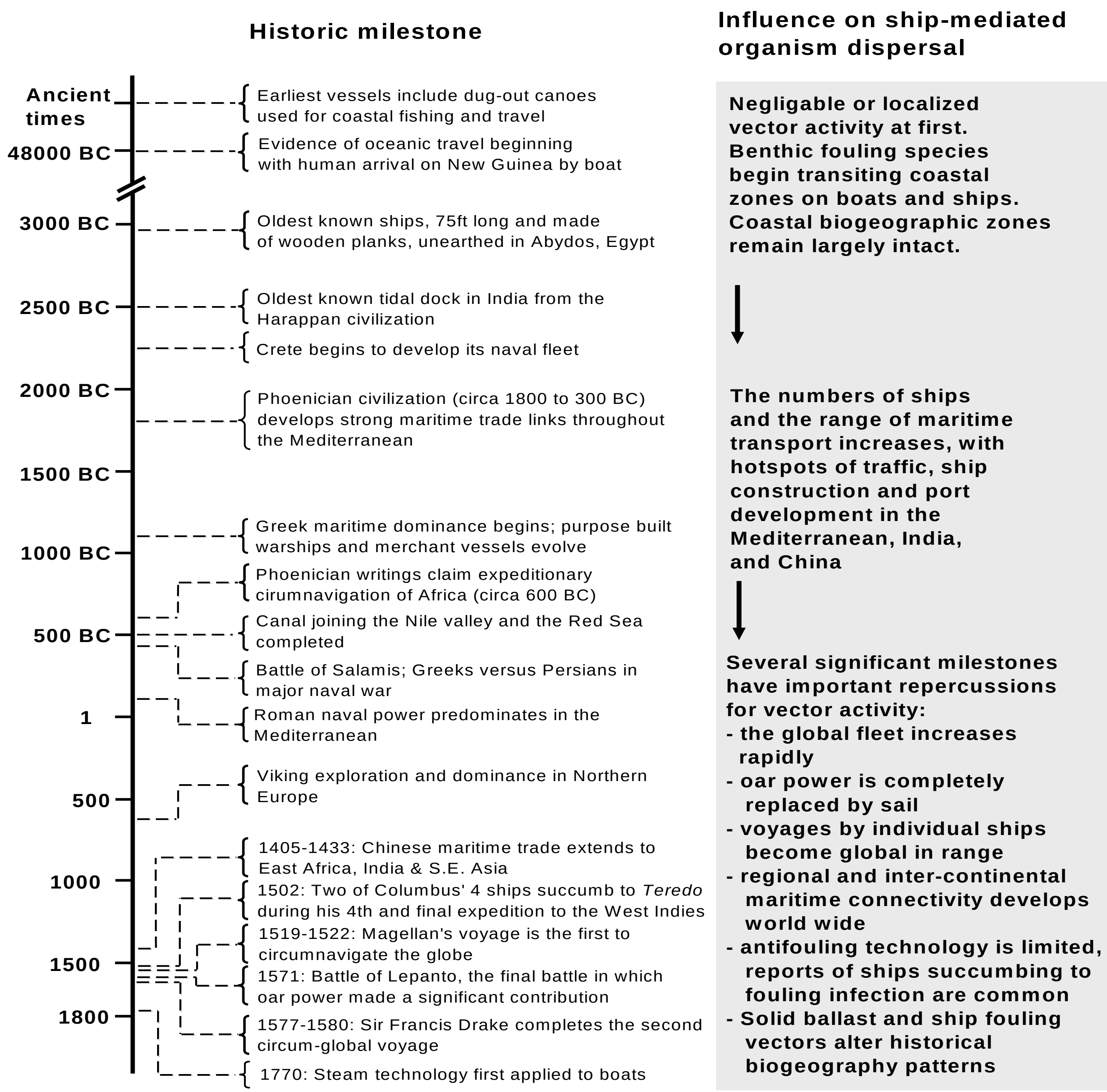
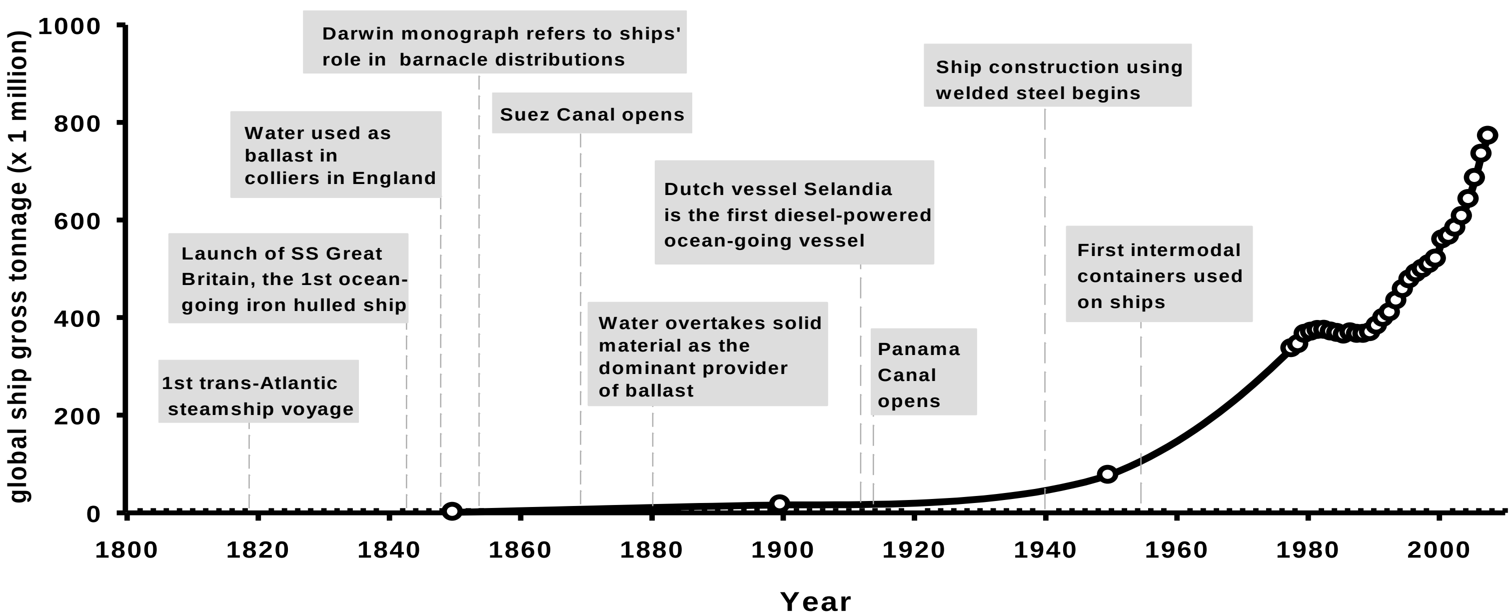


Figure 2. Vessel traffic and maritime history since 1800. The gross tonnage of global shipping is also shown (white circles). Historic milestones, including canal openings and major changes to vessel construction, are highlighted with dashed grey lines. Information from Darwin (1954), Lloyd (1975), Natkiel & Preston (1986), Carlton (1985), Galil (2008), and Euromonitor International (2009).



Methods

Review of ship fouling literature

The literature review included both a standardized search using the ISI Web of Science (using search terms hull fouling, ship fouling, biofouling) and an additional search of references within these papers and within grey literature. These data were used to characterize the sampling and research effort for ship fouling studies and to analyze the ecological patterns within the cumulative species records of ship fouling in the literature. After assessing the abstracts of studies identified during the Web of Science search, we categorized them into four groups to summarize the research effort. The categories included: 1) studies with original hull sampling; 2) studies solely concerned with recreational vessels; 3) studies on antifouling paints or ecotoxicology related to antifouling paints; 4) 'other' studies (including essay-type papers, management studies and studies of particular invasions where vectors are referred to in text but not sampled). When the information required for categorizing studies was not clear from the abstract, the full text of the study was consulted. Additional studies (reports and grey literature) that included original ship fouling data and were not identified in the standardized search were also used in this review and meta-analysis of ship fouling data.

Only studies that provided data from original hull sampling (i.e. new data from ships) were included in analysis. Recreational vessels were not included in this analysis. For each of the qualifying studies we tabulated: 1) date and location of sampling; 2) number and types of ships sampled; 3) whether sampling was conducted at both ends of a voyage; 4) sampling type (dry-dock, in-water) and methodology; 5) total number of species recorded; 6) identification of species recorded (at the lowest level of identification); 7) biofouling extent data (if any); and 8) whether the author noted the biogeographic status of the species sampled relative to the sampling location (native, non-native, cryptogenic, unknown).

Using this dataset, we summarized species information across all qualifying studies and evaluated total species richness for the subset that included all taxonomic groups. This latter approach excluded some studies that focused on particular species or taxa to the exclusion of other taxa and also those studies that used functional groups or coarse identifications, since these could not estimate total species richness. For the studies that remained, we evaluated: 1) the numbers of ships sampled and species richness per study; 2) species prevalence among studies; 3) taxonomic breakdown of species (frequency of occurrence of species among phyla); and 4) species richness per ship where ship-by-ship data were available. We also compared taxonomic patterns of ships sampled in the US versus the Antipodes (Australia and New Zealand), because these regions provided the most studies and offered an opportunity to assess geographical differences.

Additional analyses were conducted on subsets of studies that examined the effect of transit on biofouling and the relationship between dry-docking duration (paint age) and biofouling. For those studies that sampled a ship's hull prior to departure and upon arrival, we plotted the initial and end-point richness for each vessel. For studies that provided ship-by-ship data, we plotted antifouling paint age (duration since dry-docking) against species (or functional group) richness to assess the apparent trends of hull maintenance on biofouling accumulation. We also examined the prevalence of NIS within ship fouling communities for the subset of studies that provided biogeographic information.

Assessment of ship fouling vector strength

To further evaluate the role of the ship fouling vector in marine introductions, we examined species lists of nonindigenous invertebrates and algae from eight well-studied temperate locations (Table 1). We were not concerned about size differences between sites (individual bays versus whole coastlines) because our aim was to assess the contribution and patterns of the fouling vector across a range of areas for which data are available. Each location was studied using very similar approaches to determine nonindigenous (and cryptogenic) species lists, dates of introduction, native range of species, and probable vectors. Vector designations (for the initial introduction of a species) in each study were assigned using a broadly consistent methodology (see Ruiz et al. [2000]; Hewitt et al. [2004]). Briefly, vectors for each species were assigned based on

1) organism characteristics (e.g. adhesive stage for fouling, planktonic stage for ballast water); 2) introduction date and location coinciding with vector activity (e.g. shell fish stocking); and 3) behavior and habitat utilization (e.g. mobile species within fouling matrices). Multiple vectors can be assigned to a species and because the biofouling vector was the focus of this study, our interest in vector designations was limited to one of three categories: 1) fouling as sole vector; 2) fouling as one of several possible vectors; and 3) non-fouling vectored species.

For each regional analysis, we tabulated: 1) species identity, 2) its reported date of introduction (or detection), 3) its reported vector or vectors, and 4) its reported native range. We analyzed the taxonomic breakdown of species and their association with the ship fouling vector. We then compared NIS richness among regions and the reported influence of ship fouling as the initial vector of NIS to each region (using three vector designations outlined above). We also evaluated the temporal trend of reported NIS detections for each region. For this temporal analysis, we used a decadal time scale and assigned detection dates for each species per region using the year provided by the author of the study; or the mid-point (year) if a range of years was provided; or we did not include a species if a detection date was reported as unknown. We used SIMPER analysis (Similarity Percentages) to determine the taxa that contributed most to similarity of NIS lists among sites within each region (Europe, US, and Antipodes). Finally, we compared the native ranges (potential source regions) of NIS using biogeographic information provided for NIS lists from each of the eight locations.

Table 1. Data sources for eight temperate locations with published lists of nonindigenous and cryptogenic species used in analysis. The location, study citation and details of how species were included in analyses are shown.

Location	Abbreviation	Data Source	Notes on data used from authors' species lists
Ireland	Ireland	Minchin (2007)	species considered extinct or without current status by the author were not included; freshwater species excluded; vascular plants, amphibians & fish excluded; where possible, ship vectors were included as fouling, ballast water or both
Germany	Germany	Gollasch & Nehring (2006)	inland waters' species excluded; macrophytes, fish, ambphibians excluded; earliest date of occurrence for German coast was used
Belgium	Belgium	Kerckhof et al. (2007)	vascular plants and fish excluded
Puget Sound	PS	NEMESIS (2008)	vascular plants and fish excluded; freshwater stenohaline species excluded
San Francisco Bay	SF Bay	NEMESIS (2008)	vascular plants and fish excluded; freshwater stenohaline species excluded
LA/Long Beach	LA/LB	NEMESIS (2008)	vascular plants and fish excluded; freshwater stenohaline species excluded
New Zealand	NZ	base list from Cranfield et al. (1998); supplemental data from Biosecurity New Zealand (16 reports) series entitled "Baseline survey for non-indigenous marine species" (2006)	species recorded only from a towed oil platform and turtles were excluded; vascular plants & fish excluded; species described as not established were excluded; species recorded in NIS lists from the 16 supplemental Biosecurity New Zealand reports that were not recorded in Cranfield et al. (1998) were included
Port Phillip Bay	PP Bay	Hewitt et al. (2004)	fish were excluded

Results

Biofouling on ships

Biofouling studies

A database search identified 96 studies using title, abstract or topic keywords 'hull or ship fouling' and 'vessel biofouling'. After reviewing all 96 abstracts, there were only 6 ship fouling studies that included original sampling of vessel hulls. A large majority of the 96 studies identified by the search focused on antifouling paints and ecotoxicology issues (Fig. 3). Three studies of recreational boat fouling were found in the search results (e.g. Floerl et al., 2004). Additional 'other' studies, including studies referring to ship fouling (e.g. Coutts et al., 2007) or to particular NIS (e.g. Golani, 2004), did not involve new data from sampling of ships' submerged surfaces.

When this literature search was combined with our own database (including grey literature), we identified a total of 36 different studies in which samples (collections or photographs) were taken from ships' submerged surfaces. There were at least 863 ships sampled, but some studies did not report the numbers of ships so this is an underestimate of the total from these studies. The earliest of the 36 studies was published in 1910, but more than half (53%) were published or released since 2000 (Fig. 4). The United States (14 studies) and the Antipodes (10) were the dominant regions where vessel sampling took place, with other studies conducted in the NW Pacific (China, Japan, Eastern Russia [4]), Europe (3) and Brazil (1). A further three studies reported findings from samples collected at a variety of widespread (global) locations. In addition to timing and geography, studies differed in sampling methodologies, type of access to vessel hulls, the numbers of vessels sampled, area of hull sampled and taxonomic focus. Despite this, sub-groupings of studies with similar approaches and presentation of results were suitable for data synthesis.

Three of the studies used photographic methods to analyze hull fouling and therefore used functional groups rather than taxonomic identification in analysis. For the remaining 33 studies, there was a total of 1598 species (or taxa) records. After accounting for synonymy, these records represented 1128 distinct organisms; 729 different species and an additional 399 distinct organisms not identified to species or genus level. These species and taxa represented 21 different phyla or divisions ranging from single-celled protozoa to fish, but primarily macro-invertebrates. Because some studies were focused on specific organisms, taxonomic bias precluded comparisons among phyla or species groups using all 33 studies. Specifically, eight studies limited their hull investigations to barnacles (3), algae (2), selected crustaceans (1), polychaetes (1), and a flatworm (1) (Chilton, 1910; Bishop, 1951; Foster & Willan, 1979; Callow, 1986; Bagaveeva, 1988; Faubel & Gollasch, 1996; Mineur et al., 2007; Otani et al., 2007). A further five studies examined an assortment of targeted taxa and did not attempt to characterize the full diversity of fouling organisms on the vessels being sampled (Allen, 1953; Arias & Morales, 1963; Huang Xiuming et al., 1979; DeFelice & Godwin, 1999; Zvyagintsev, 2003). There was a subset of 20 studies, however, that did not narrow their taxonomic focus and recorded all macro-invertebrates and algae encountered during their sampling.

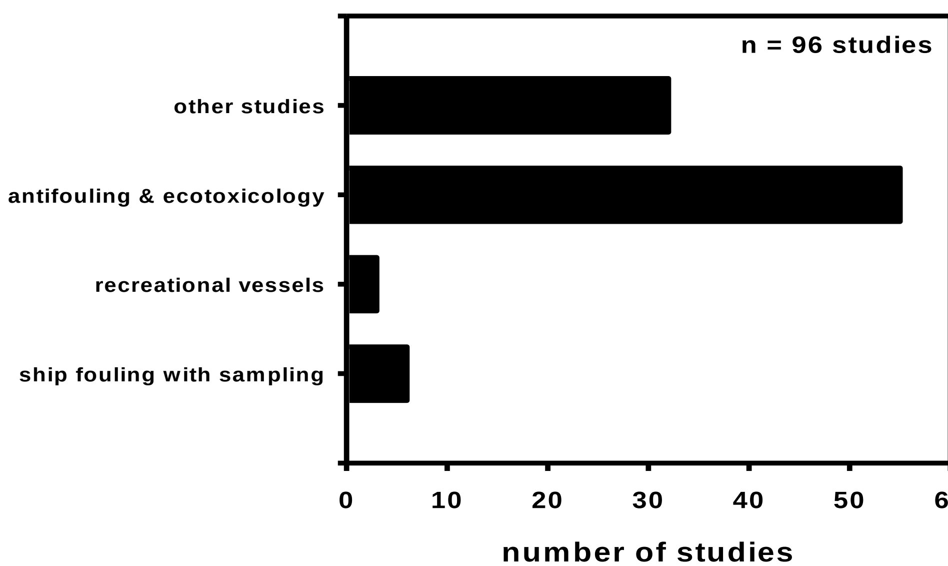


Figure 3. Comparison of topics examined in published ship fouling studies. These data are from a literature search using Web of Science and encompassing the period between 1955 and February 2009. Ship fouling literature was searched using the terms 'hull OR ship fouling' OR 'vessel biofouling'. Studies were assigned to one of four categories after assessing the abstracts of all 96 papers. Just six studies involved original data collected from the submerged surfaces of ships.

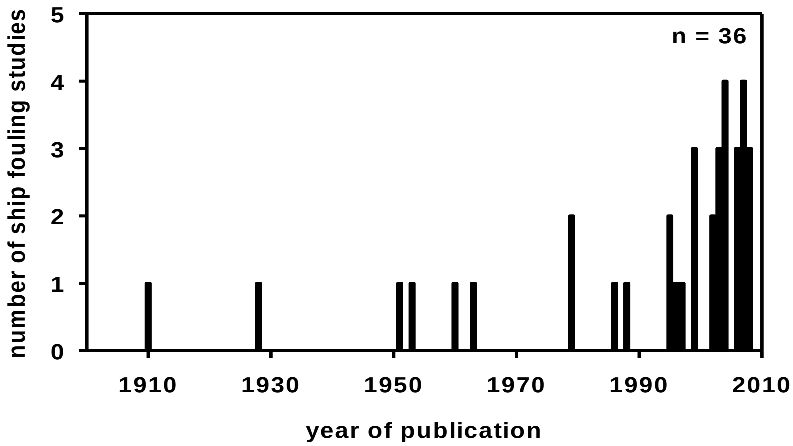


Figure 4. Temporal trend of ship fouling studies. The number of studies per year (of publication) is plotted for 36 papers/reports with original data from ships' submerged surfaces.

Taxonomic and richness comparisons in ship fouling studies

The combined number of species records (which can include the same species recorded across several studies) from these 20 studies amounted to 1381 from 447 ships (Fig. 5). Visscher (1928) had the highest number of ships sampled (250), but richness data was only presented for 100 ships. The only other study to report data from 100 or more ships was Gollasch (2002), which provided data on 131 ships sampled in Germany. Most studies (14) reported data from 10 or fewer vessels. The highest number of species recorded in a single study was 124 sampled by Godwin et al. (2004) in a study of 35 vessels in Hawaii. Eight single-vessel studies accounted for 42% of the species records among the 20 studies (Fig. 5), and single-vessel studies were focused on unusual or stochastic ship movements (such as decommissioned ships).

There were 904 different species (or taxa) identified within the 1381 species records. Seventy-seven percent of the (904) species were singletons (occurred in just one study each), which represented 50% of all species records among studies (Fig. 6). There was a significant difference between phyla in their contribution to species richness ($\chi^2_{(20)}$ = 2345.2, $p < 0.001$; Fig. 7). The five highest ranked phyla accounted for over 75% of the species recorded. Arthropods were the most speciose phylum with 298 species recorded from 501 records. There were 73 different barnacles and *Amphibalanus amphitrite* was recorded in 18 of the 20 multi-taxon studies, by far the most commonly reported species sampled (see Fig. 6). Forty-two barnacle species did not occur in more than one study. Annelids were the next most recorded phylum (184 records) but molluscs were the second most species rich phylum (134 species; Fig. 7). Molluscs and sponges had the highest ratios of species richness to records number, indicating that they had the highest rate of singletons. Barnacles had the lowest percentage of species per records (41%).

Where ship-by-ship richness data were available (n = 362 ships), a majority had five or fewer species (59%; Fig. 8), including 30 ships with zero biota. The maximum recorded richness of 115 species occurred on a decommissioned ship and the highest values for in-service ships were 72 and 36 for a dry-docked and in-water vessel, respectively. Up to 45% of the species recorded within fouling communities of all 20 studies were mobile (unattached) species. The exact mobile to sessile ratio cannot be determined because many taxa were not identified sufficiently, but polychaetes and amphipods were the most numerous unattached taxa.

Regional comparisons of fouling taxa were made between studies conducted in the USA versus the Antipodes because: 1) both regions had several studies among the 20 multi-taxon studies (nine versus six studies, respectively); and 2) both regions incorporated sampling of stochastic vessels, dry-dock sampling and in-water sampling. Five out of eight taxa groups were recorded more frequently from US studies compared to Australia and New Zealand (Fig. 9). The only taxa that had greater than a 2:1 ratio between regions, however, were sponges and ascidians, which were recorded 4.5 and 5 times more often (proportionally) in Southern Hemisphere hull sampling.

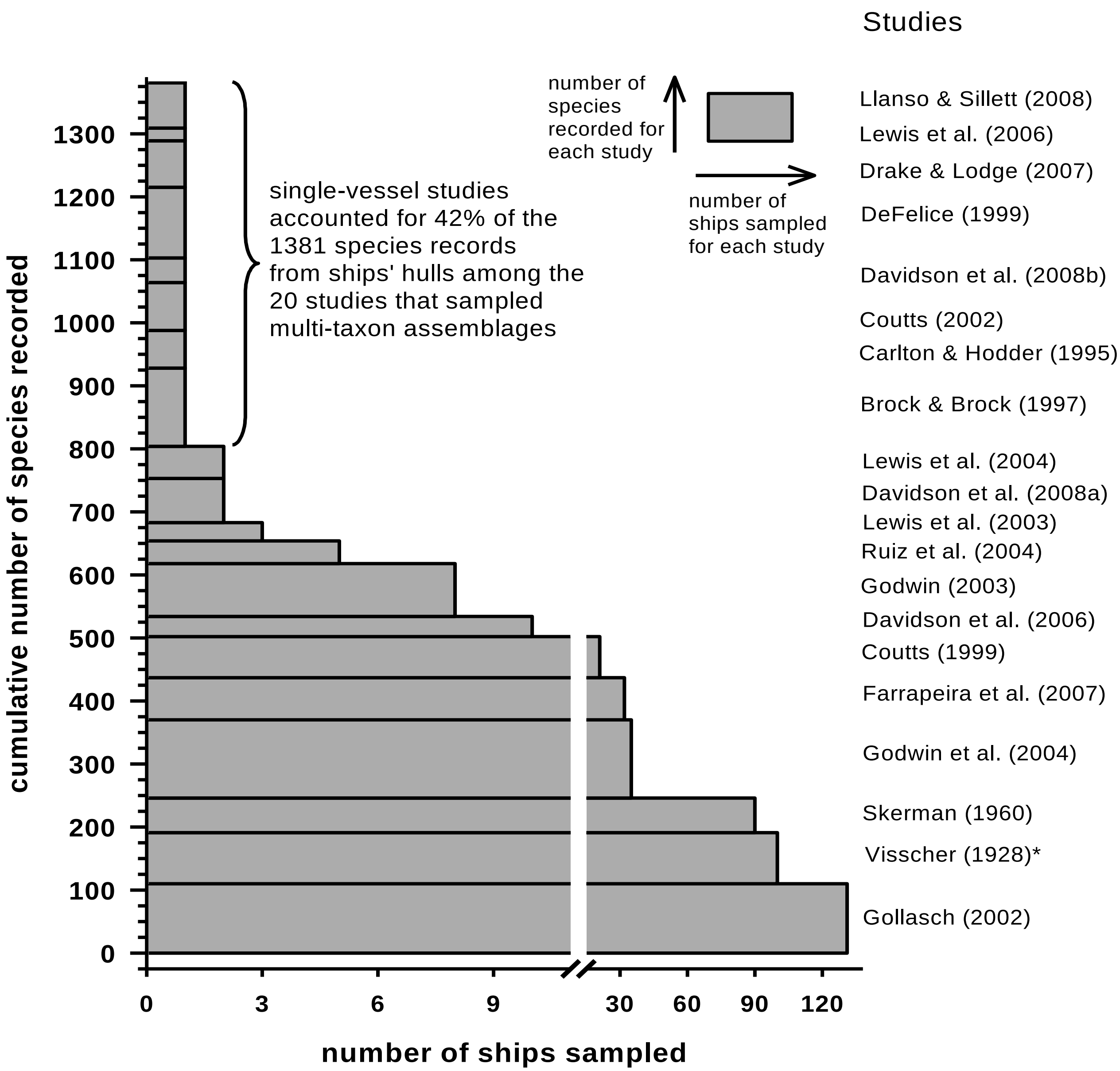


Figure 5. Number of ships sampled and species richness for multi-taxon ship fouling studies. 20 different studies sampled ship fouling organisms and did not restrict their sampling to particular taxa. For each horizontal bar, the corresponding study is listed on the right. The Y-axis represents the cumulative number of records of species and not cumulative species richness (i.e. some species were recorded in several studies and all occurrences are included). *250 ships were sampled in Visscher's study but richness per ship is only provided for the first 100.

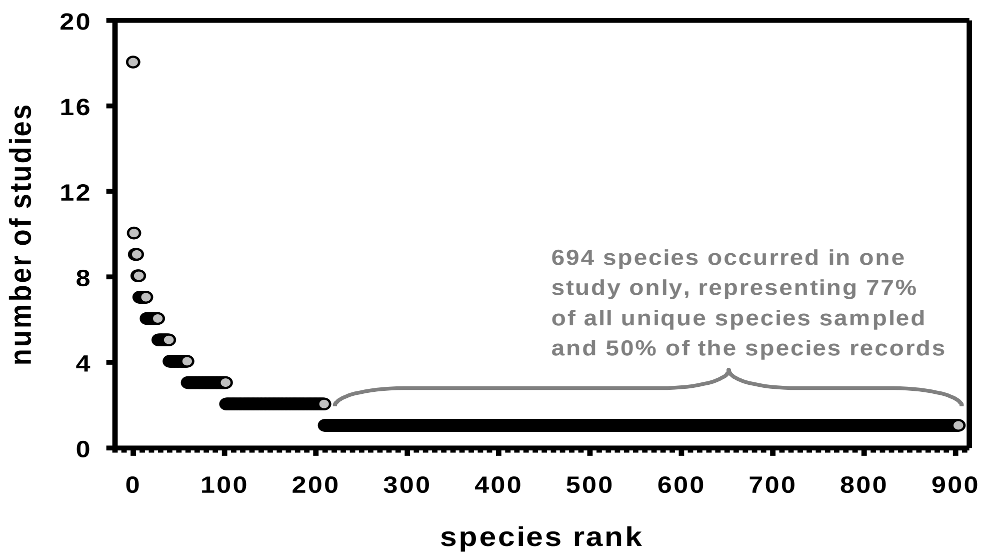


Figure 6. Species records among 20 multi-taxon studies. Species are ranked in order from most common to least common in terms of numbers of studies they appeared in (from L to R). *Amphibalanus amphitrite* was the most widely recorded species (ranked number 1), occurring in 18 of 20 ship sampling studies. The high incidence of singletons (species that occurred in just one study) contributed to 1/2 of overall richness.

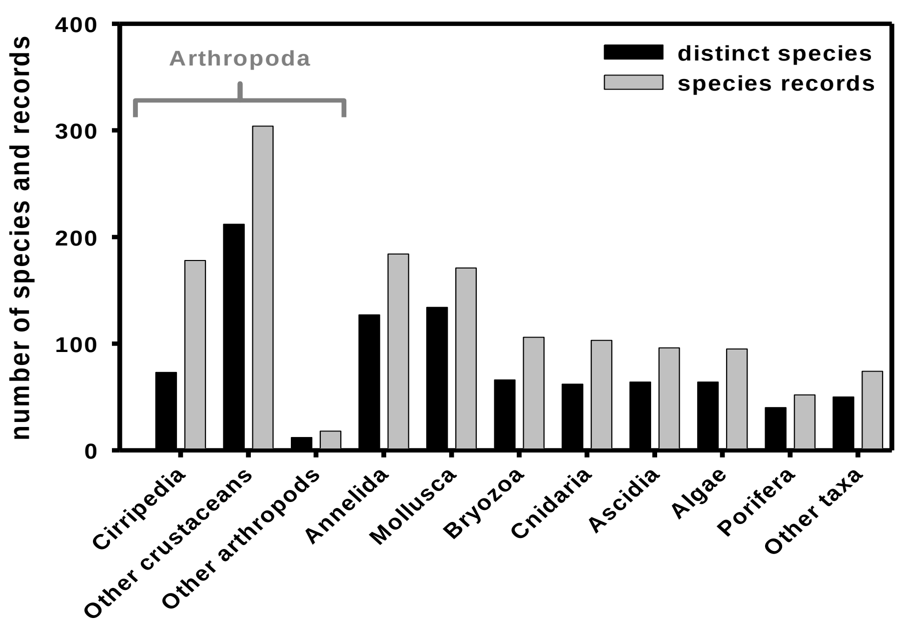


Figure 7. Comparison of species richness and species records among taxa. The taxonomic breakdown of species richness (n=904, black bars) and the number of records per taxon (n = 1381, grey bars) is shown.

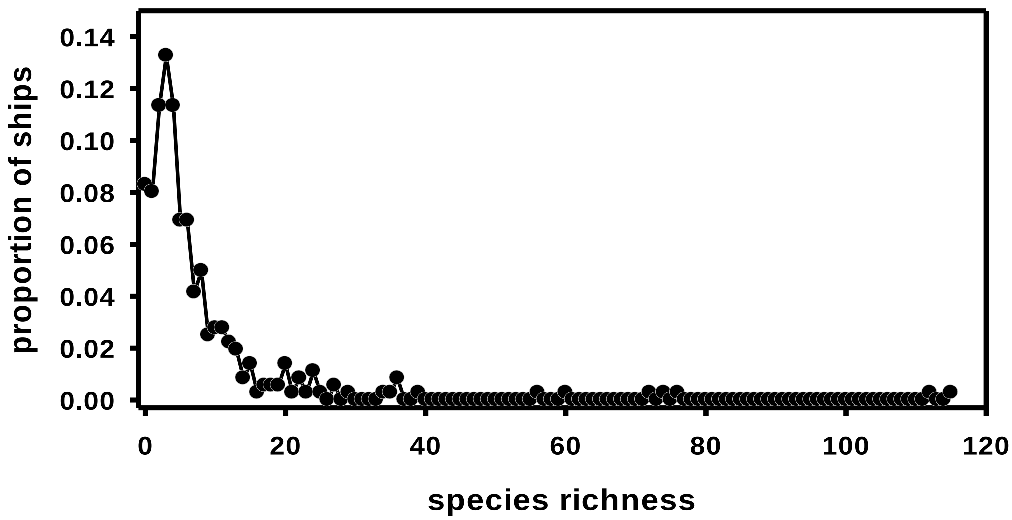


Figure 8. Species richness on ships' hulls. Histogram of species richness in biofouling communities of vessels for which data were available (n = 362).

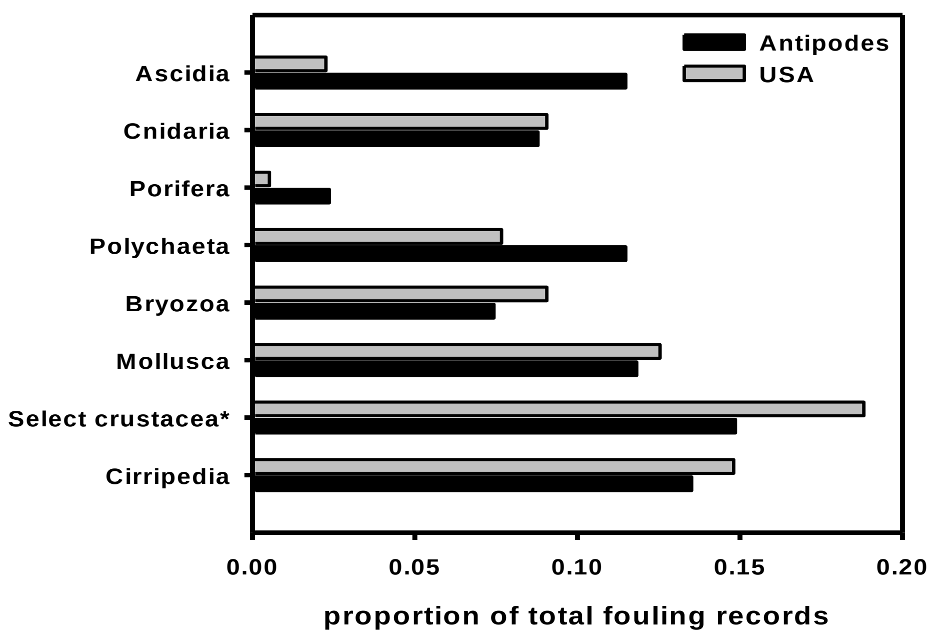


Figure 9. Comparison of frequency of taxa records between two regions. The proportion of species records from ship fouling among 8 taxa groups is shown for US (9) and Antipodean (6) studies. Black and grey bars represent Antipodean and US regions, respectively. The 8 taxa groups listed represented over 75% of the total fouling records for both regions (n = 574 and 296 records for US and Antipodean regions, respectively). *Select crustacean refers to decapods, amphipods and isopods.

Voyage and vessel maintenance effects on ship fouling vectors

Repeat sampling of the same vessel before and after a voyage has only been reported for 9 voyages in 5 different ship fouling studies. The voyages varied by location, duration and distance traveled and conditions included passage through freshwater (e.g. Panama Canal) and sea-ice. Changes in species richness between departure and arrival port surveys among the nine voyages were highly variable (Fig. 10). Two ships reached their destinations with more than a 50% increase in richness, two more voyages resulted in greater than 80% decreases in richness, and the remaining five recorded an end-point difference of less than 10% compared to initial sampling.

Some measures of pre- and post- voyage biofouling extent (or abundance) were also made for most of the nine voyages. A bryozoan, *Conopeum chesapeakensis*, was a dominant primary fouling species on 2 vessels traveling from San Francisco Bay to Texas, via the Panama Canal (voyages 7 and 8, Fig. 10b). Its average abundance of 60% cover of the hull surface reduced to less than 3% upon arrival. The third vessel that underwent the same voyage reported a much lower initial percent cover (1% to 5%) of the same species in samples upon departure and a broader range of cover at the end-point of the voyage (1% to 32%). The numerical abundance of dominant amphipods (*Corophium spp*) on two short US West Coast transits did not change significantly (voyages 2 and 3, Fig. 10b). Stark reductions in biomass were reported qualitatively for another vessel that transited between Puget Sound and Hawaii (voyages 4, Fig. 10b). For two Antarctic voyages (5 and 9, Fig. 10b), one resulted in a 100% clearance of all biota and the other had no significant change in biofouling extent.

There were 163 vessels within the 36 fouling studies that reported duration since dry docking (paint age) and some measure of richness. The general trend of increased richness with increased paint age was apparent, although some taxonomic groups with fewer data points did not show such clear relationships. For example, there was no significant correlation between paint age and algal richness on ships sampled in the Mediterranean (Pearson's correlation $r^2 = 0.03$, $p > 0.05$; Fig. 11a). There was a significant correlation between taxonomic groups and paint age of ships sampled in

Oakland, California (Pearson's correlation, $r^2 = .35$, $p < 0.01$). Analysis showed there was no significant difference in species richness between ships sampled prior to 1928 and after 1990 after the effect of paint age was accounted for (ANCOVA, $F = 0.91$, $p > 0.05$). Overall the correlation between species richness and paint age was significant (4 studies; $r^2 = 0.16$, $p < 0.001$). There were insufficient meta-data to analyze the patterns of additional factors such as paint type or vessel speeds on richness.

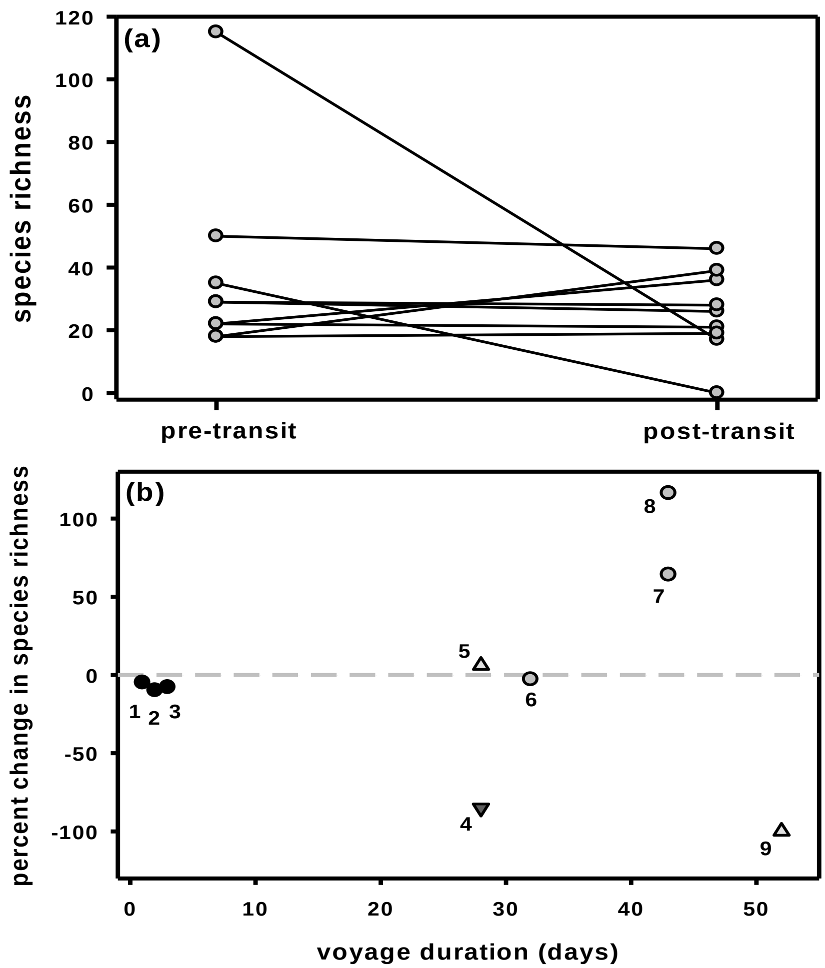


Figure 10. Effect of transit on ship fouling richness. (a) Estimates of species richness before and after voyages for nine voyages and (b) the percentage difference in species richness and the duration of these voyages are plotted. Numbers correspond to voyages from 1) Yaquina Bay to Coos Bay, Oregon; 2) Coos Bay to Humboldt Bay, California; 3) Humboldt Bay to San Francisco Bay, California; 4) Puget Sound, Washington to Hawaii via Astoria, Oregon; 5) Fremantle to Hobart, Australia via Heard Island, Antarctica; 6, 7 and 8) San Francisco Bay to Brownsville, Texas; 9) Hobart, Tasmania to Casey Station, Antarctica and back. Data are from Carlton & Hodder (1995)[voyages 1, 2, 3]; Davidson et al. (2008a)[7, 8];

Llanso & Sillett (2008)[6]; Lewis et al. (2004)[5, 9]; and Brock et al. (1999) with additional input from DeFelice & Godwin (1999)[4].

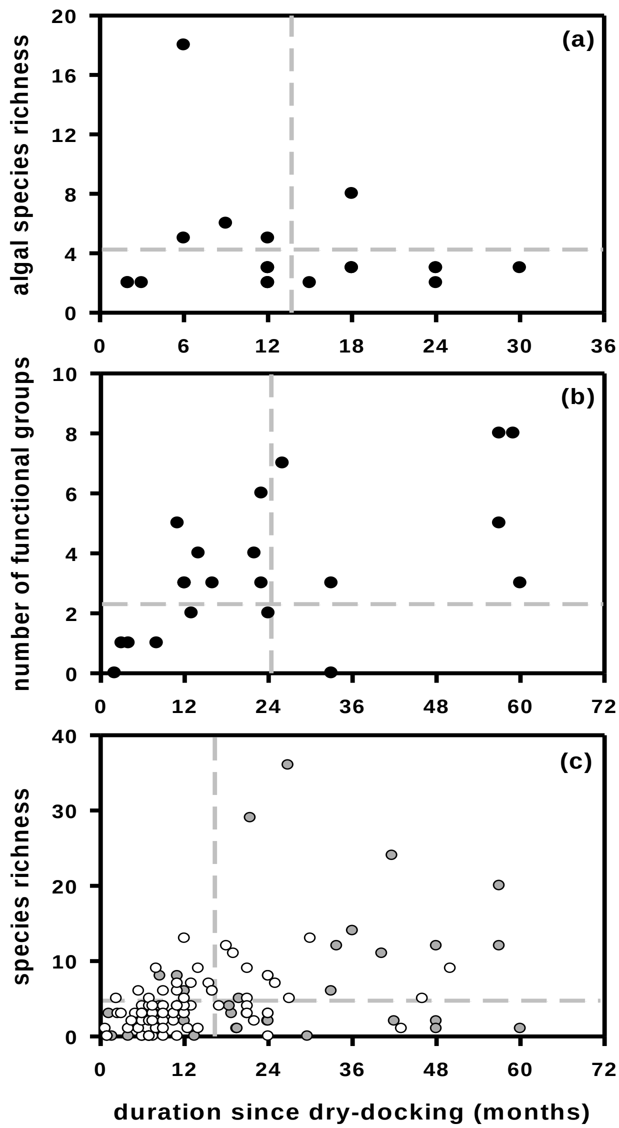


Figure 11. Ship fouling richness and antifouling paint age (duration since dry docking). Plots of algae richness (a), functional group (b) and species richness (c) are shown in relation to duration since docking. Functional groups are broad taxonomic categories (e.g. barnacles, hydroids, etc). Data are from: (a) Mineur et al. (2006); (b) Davidson et al. (2007a); (c) Visscher (1928), Coutts (1999), Ruiz et al (2004), and Davidson et al. (2006). Dashed lines represent the mean values of richness and paint age in each plot. White and grey circles in plot (c) represent data collected before 1928 and after 1996, respectively.

Nonindigenous species (NIS) in hull fouling

Twenty-three of all 36 fouling studies reported NIS on 377 occasions on the hulls of sampled vessels; the others did not provide any biogeographical details. There were 276 different species reported as non-native and 62 of these were recorded more than once among studies. There were 107 arthropods, including 54 barnacles, listed as non-native within fouling communities. The highest percentages of non-native records within taxa occurred for barnacles (39%), bivalves (38%), ascidians (37%) and bryozoans (34%). Among mobile taxa, isopods (26%), amphipods (26%) and decapods (20%) had the highest number of records of nonindigenous species. *A. amphitrite* was recorded as non-native in nine studies and five other members of the *Amphibalanus* genus were recorded as non-native more than once. Two bryozoans, *Bugula robusta* and *Schizoporella unicornis*, were recorded in 5 different studies as non-native. The highest number of NIS was recorded by Gollasch (2002), where 74 of the 110 species sampled on ships' hulls were not native to the coast of Germany. Three studies conducted in Hawaii also reported high proportions (34% - 56%) of non-natives among the species sampled (DeFelice, 1999;Godwin, 2003; Godwin et al., 2004).

The role of ship fouling in NIS distributions at eight locations

There were 838 records of invertebrate and algal NIS, representing 553 different species, among the 8 temperate locations examined (these data are not from ships' hulls but from lists of established species at each location). The most speciose groups included arthropods (129), molluscs (75) and bryozoans (56). Only two species, *Caprella mutica* and *Styela clava*, occurred in 7 of the 8 locations, while 403 species occurred in just one site each. Ship fouling was a sole or possible vector for 73% of the 553 species. The fouling vector played a prominent role in the transfer of species within most taxonomic groups and was associated with more than 90% of the NIS in several groups including algae, sponges, bryozoans, cnidarians and ascidians (Table 2). The 22 most widespread species - those that occurred in five, six and seven locations – accounted for 121 distinct records of introductions among all 8 locations. The fouling vector was recorded as a sole or possible vector for 104 (86%) of these recorded incursions of widespread species.

New Zealand, PP Bay and SF Bay had significantly higher numbers of NIS than other locations ($\chi^2_{(7)} = 182.75$, $p < 0.001$; Fig. 12a). The proportions of NIS that were considered fouling-mediated also differed among locations ($\chi^2_{(7)} = 108.7$, $p < 0.001$), with New Zealand, PP Bay and LA/Long Beach having notably higher percentages than the other 5 locations (Fig. 12b). The best fit relationships of cumulative NIS increase through time for all eight locations was an exponential function (all $r^2 > 0.82$, all $p < 0.001$). The decadal trend for fouling mediated species (fouling as sole or possible vector; Fig.13) throughout the 1900s was a linear function for SF Bay and Germany (all $r^2 > 0.96$, all $p < 0.001$) and exponential for the other six locations (all $r^2 > 0.77$, all $p < 0.001$). The fouling vector was associated with an average of 70% (standard deviation = 9.6%) of total NIS incursions per decade across all locations over the same 100 year period (Fig. 14). The largest decadal increases of NIS incursion for each location occurred after 1960, with the highest occurring during the 1970s at PP Bay when 56 new NIS were detected (just 11% of these were not linked to fouling vectors). Since 1990, 67% of 207 new NIS that were detected across all locations were considered possible fouling incursions, 29% unambiguously so.

Pacific Asia was the top ranked donor region to the three US locations (Table 3). PP Bay and New Zealand had a high percentage of NIS from European or NE Atlantic native ranges, while most NIS at European sites were native to the North Pacific or NW Atlantic. SIMPER analysis (using broader taxonomic groups such as amphipod, gastropod etc) revealed that European sites were characterized by bivalves, annelids and red algae; amphipods, ascidians and bivalves distinguished American sites; while bryozoans, hydroids and sponges were the major contributors to Antipodean site similarity. Green algae, cnidarians, ascidians and barnacles had the highest affinity to the fouling vector (see Table 2), but there was no significant difference among sites in percentage of NIS richness from these groups ($\chi^2_{(7)} = 5.12$, $p > 0.05$). Eighty-percent of non-native molluscs and arthropods at LA/Long Beach were fouling-associated. In New Zealand, the value was 90%. In contrast, although SF Bay had double the number of non-native arthropods and molluscs (91) compared to all other sites, the fouling vector was linked with just 44% of them. Likewise, 39% of these two phyla in Puget Sound were linked to fouling vectors.

Table 2. Taxonomic and vector comparisons for NIS distributed at 8 temperate locations. For each taxon, the number of species recorded and their association with the ship fouling vector are shown. The last column (furthest right) shows the percentage of species in each taxon that were considered to have fouling as the sole vector or as a possible vector combined (fouling as sole + possible vector). The compilers of NIS lists at each location considered only 27% of species to have no link to the fouling vector during the initial introduction.

phylum / division / kingdom	taxon	number of species per taxon among all 8 locations	vectors			% of taxon with fouling-associated species
			fouling alone	fouling included with others as a vector	non-fouling	
chlorophyta	green algae	16	10	6	0	100.0
phaeophyta	brown algae	39	32	6	1	97.4
rhodophyta	red algae	47	31	12	4	91.5
porifera	sponges	31	14	15	2	93.5
annelida	annelids	46	12	16	18	60.9
ectoproct	bryozoans	56	34	21	1	98.2
echinodermata	echinoderms	2	0	1	1	50.0
platyhelminthes	flatworms	3	2	0	1	66.7
cnidaria	anthozoans	8	2	6	0	100.0
	hydrozoans	40	17	23	0	100.0
	scyphozoans	1	0	1	0	100.0
arthropoda	barnacles	11	8	3	0	100.0
	amphipods	40	12	21	7	82.5
	isopods	16	7	6	3	81.3
	decapods	19	6	5	8	57.9
	copepods	24	0	4	20	16.7
	insects	7	1	1	5	28.6
	other arthropods	12	0	1	11	8.3
mollusca	gastropods	38	3	12	23	39.5
	bivalves	37	12	8	17	54.1
urochordata	ascidians	27	27	0	0	100.0
protista	protists	13	5	1	7	46.2
	other taxa	20	0	1	20	5.0
Total		**553**	**235**	**170**	**149**	**73.2**

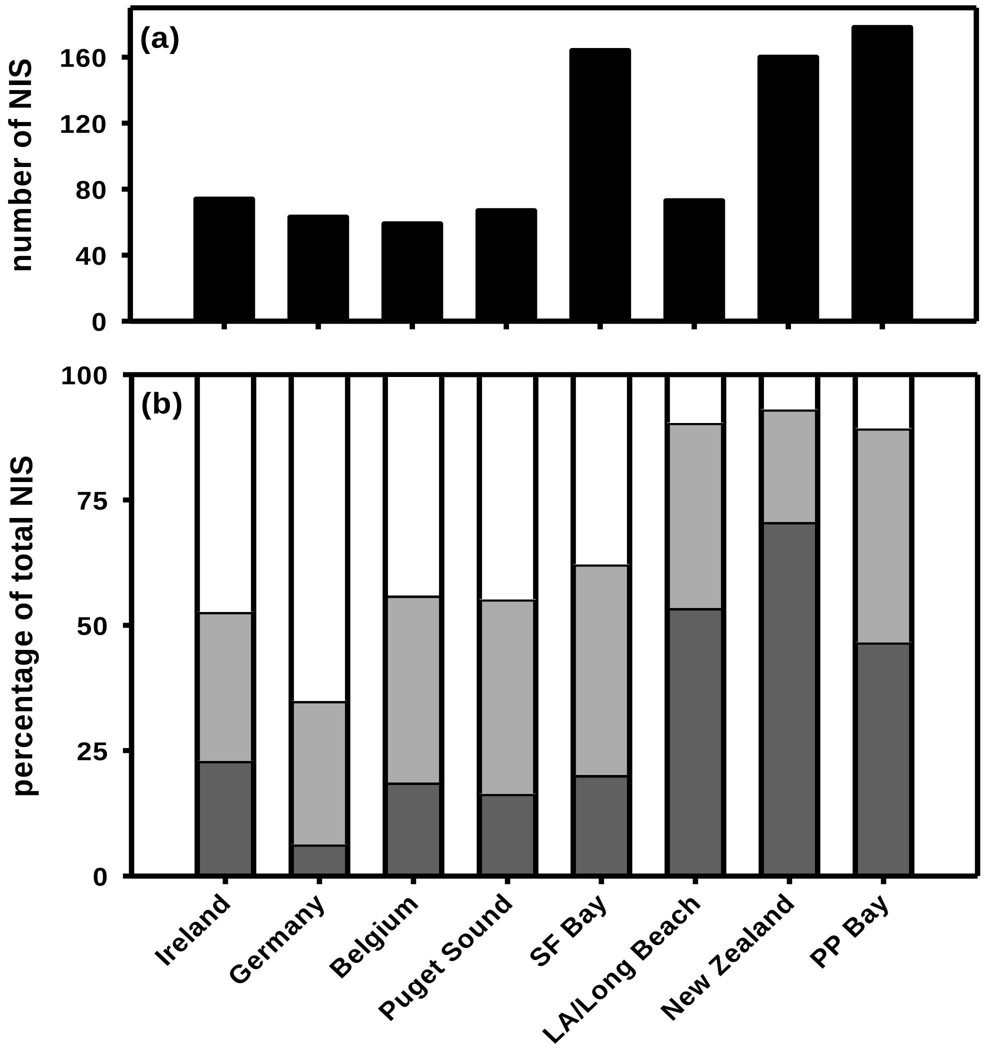


Figure 12. NIS and fouling vector comparisons between locations. (a) The number s of NIS for each site and (b) the contribution of fouling vectored species to the totals. In plot (b), dark gray represents the proportion of species considered to have been transferred by fouling alone; light grey represents the proportion that included fouling as a possible vector; and white represents the proportion of species considered to have no link to the fouling vector during the initial introduction.

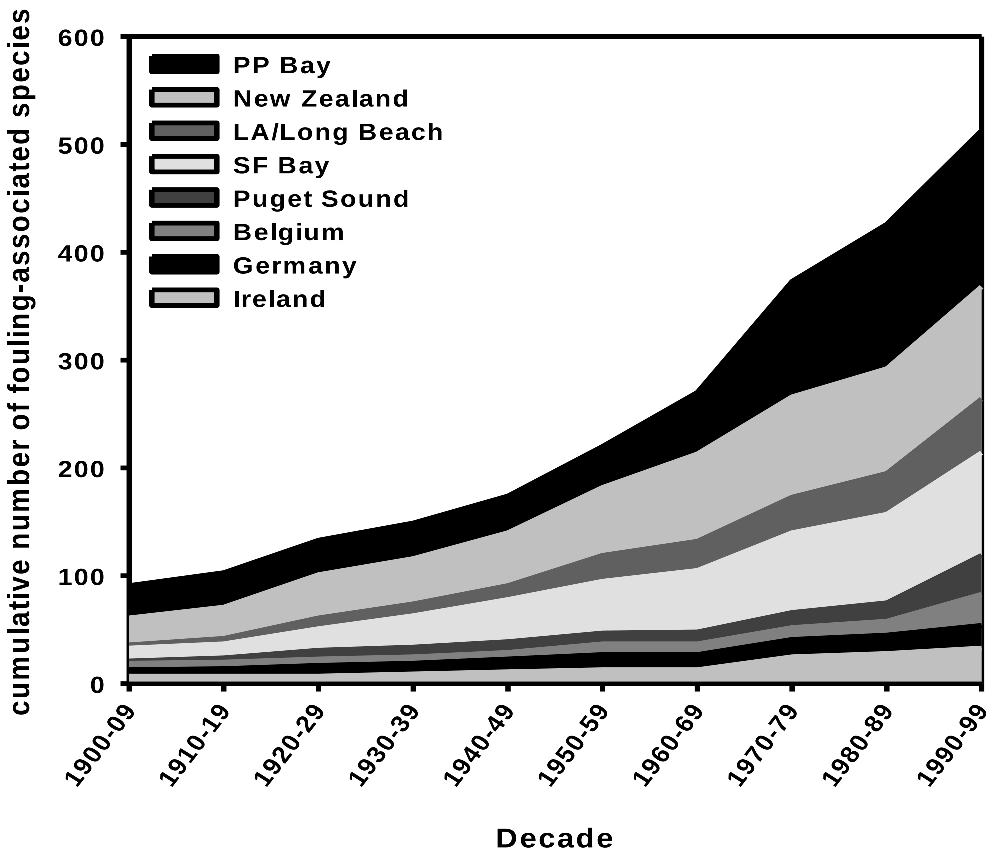


Figure 13. Temporal trends of fouling-mediated NIS for eight locations. The cumulative number of fouling-mediated species, those whose incursion vector was attributed to fouling alone or as a possible vector, is shown (n = 513). Species whose introduction or detection date was prior to1900, after 1999 or unknown are not included. The best-fit relationships for all locations was an exponential function except for Germany and SF Bay (see text).

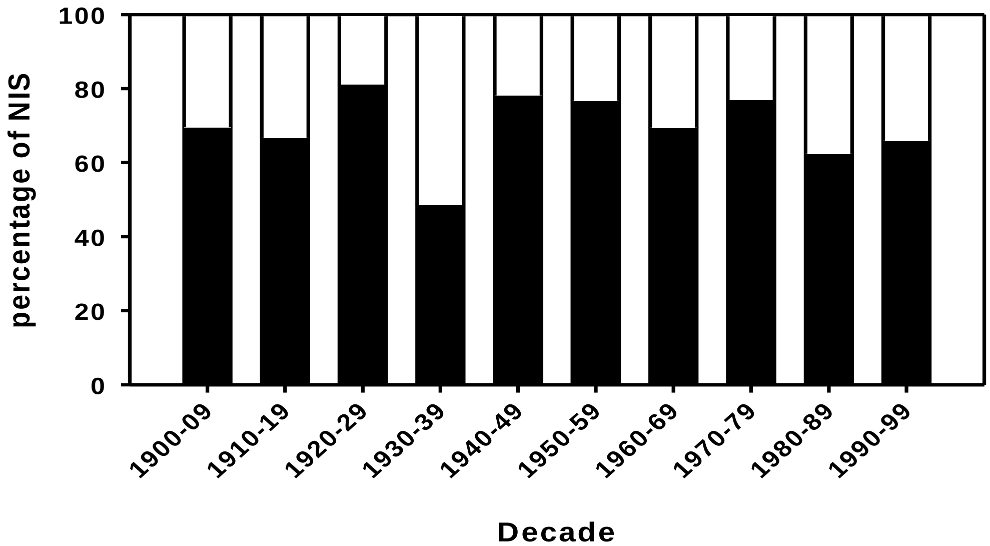


Figure 14. Decadal trends of fouling-mediated NIS for eight locations combined. For each decade of the 1900s, the percentage of NIS that was associated with fouling across all eight sites is shown. Black (filled) portions of bars represent the percentage of total NIS that had fouling a sole or possible vector. White (unfilled) portions of the bars represent the percentage of NIS not associated with fouling (unambiguously). Pre-1900 and post 1999 data are not included. Species with unknown dates of incursion (or first detection) are also not included. This plot represents 626 (75%) of the 838 species listed for all eight locations.

Table 3. The relative proportions of native ranges (possible donor regions) of NIS for 8 locations. The highest proportion of species from native ranges is highlighted for each location (e.g. 38% of Puget Sound's NIS is considered native to Pacific Asia).

NIS native range	Ireland	Germany	Belgium	Puget S	SF Bay	LA/LB	NZ	PP Bay
NE Atlantic	10%	5%	6%	8%	7%	3%	**26%**	**38%**
Atlantic N. America	10%	27%	**27%**	14%	12%	12%	6%	4%
Atlantic (other)	6%	0%	0%	19%	13%	14%	0%	9%
Pacific Asia	**21%**	14%	24%	**38%**	**26%**	**27%**	9%	7%
Pacific N. America	8%	0%	0%	0%	0%	0%	6%	5%
Pacific S. America	0%	0%	3%	0%	1%	2%	1%	1%
Antipodes	5%	0%	3%	0%	3%	3%	10%	1%
Pacific (other)	10%	**32%**	9%	0%	0%	0%	1%	1%
Indian Ocean	0%	0%	0%	0%	0%	0%	0%	2%
Ponto-Caspian	5%	14%	3%	0%	0%	0%	1%	0%
South Africa	0%	0%	0%	0%	0%	0%	3%	0%
Cosmopolitan / unreported / unknown	25%	9%	24%	22%	38%	39%	38%	31%

Discussion

Fouling communities on ships

Ship fouling has arguably had the greatest longevity of all unintentional NIS vectors in the world. A historical record that dates back several millennia is a formidable duration for human-mediated species dispersal and one of the primary causes of invasions within coastal marine ecosystems. While much of the timeline of species re-distributions by ships went unrecorded throughout history (Carlton & Hodder, 1995), biofouling now has an ecological literature extending back at least 150 years, albeit an uneven and sparse record. There has been a resurgence of ecological research interest in ship fouling over the past decade, however, and the increased research output has been widely distributed globally. This has helped to address a gap in research that developed throughout the TBT-era (the time when tributyl tin was the predominant biocide used in antifouling paints) during a time when ballast water was strongly favored for academic and applied attention (Nehring, 2001; Godwin, 2003; Mineur et al., 2007). The relatively recent inclinations to demote ship fouling as a bygone vector of lower priority because of developments in shipping and antifouling (Carlton, 1985) has subsided because of management concerns over non-ballast vectors. In particular, there is concern that effective management that may lead to a reduction in ballast-mediated introductions may not reduce the overall introduction rate if other vectors continue unabated (Fofonoff et al, 2003; Drake & Lodge, 2007). Of course, antifouling technology remains an important and widely studied research topic (Fig.3), but the number of introductions historically and new introductions recently resulting from ship fouling transfers has helped focus attention on the enduring impact of the vector and reignite ecological and biogeographic interest in it.

The high diversity of marine organisms recorded in biofouling communities, both at species and higher taxonomic levels, reflects the wide range of entrainment potential for the vector. A majority of the world's animal phyla occur in the sea (32 of 33; May, 1994), and 13 invertebrate phyla (including urochordates) have been recorded in ship fouling communities. Additional taxa documented on ships' submerged surfaces include many types of algae, cyanophyte bacteria, foraminifera, plants and benthic fish. While the number of distinct taxa (mainly species) recorded on hulls reached a substantial 1128 in the reviewed literature, this is undoubtedly made up of a minimum estimate for most groups and a significant underestimate for poorly studied groups. Moreover, assessment of microorganisms (including spores and resting stages) is virtually unexplored for hull biofouling assemblages (but see Callow, 1986), just as in assessments of established invasions in coastal ecosystems (Ruiz et al., 2000).

Amphibalanus amphitrite was the most frequently recorded species among ship fouling studies and was recorded by Darwin on the hulls of many ships arriving to Britain from the West Indies and West Africa (Darwin, 1854). This barnacle has also been recorded on ships' hulls sampled at ports in New Zealand, Tasmania, Western Australia, China, Japan, Eastern Russia, Hawaii, Brazil, Germany, Spain, and the East, West and Gulf Coasts of America (this review). As such, the species provides a case study of organism characteristics that best utilize ships as a method of dispersal, additional to its natural means, for an organism whose adult life-stage has no dispersal capability. These characteristics include voluminous propagule production, adhesion and hardiness associated with many acorn barnacles in addition to its species-specific traits of wide temperature (1.5-40˚C) and salinity (10-52‰) tolerance (Zullo 1966; Ritz & Foster, 1968; Anil et al., 1995; Cohen 2005). It comes as no surprise, then, that the boundaries of its native range in the Indo-West Pacific are somewhat unresolved given its historical prevalence in ship fouling communities (Paul Fofonoff, pers. comm.). The current distribution in the North and South Atlantic and Pacific, including the Mediterranean and Caribbean, is probably the result of centuries of ship fouling transfers. Its larval duration ranging between 6 and 18 days (at 15˚C and 30˚C, respectively) means it can also be re-distributed in ballast water, though records of *A. amphitrite* within much of its non-native range pre-date the ballast water vector (Davidson et al., 2007b).

Other widely recorded species from hull sampling within the literature include *Amphibalanus improvisus*, *Elminius modestus*, *Conchoderma auritum* (barnacles), *Obelia dichotoma* (hydroid), and the (mobile) amphipod *Monocorophium ascherusicum*. Each of these species has a broad non-native range, some along coastlines of several continents, while *C. auritum* is a cosmopolitan oceanic barnacle often recorded on marine mammals as well as ships. The two most commonly recorded bryozoans, *Bugula neritina* and *Watersipora subtorquata*, occurred in 8 and 6 studies, respectively. Both of these species are heavy-metal tolerant, a trait that provides obvious benefits to species that colonize ships' submerged surfaces because of the toxicity in antifouling paints (Floerl et al., 2004; Piola & Johnston, 2006). Biocide tolerance has also been shown to aid the establishment of species that are introduced to harbor environments, where pollution is generally high, by improving competitive outcomes against metal-sensitive native species (Piola & Johnstone, 2008). In these instances, ships are a key component in altering biotic systems by acting as a transfer mechanism, providing a substratum that can influence (increase) metal tolerance of organisms and possibly contributing to polluted conditions in some harbor environments that appear to favor some of the species transferred. Another aspect of *W. subtorquata*'s tolerance of antifouling paints is that its morphology (colonial encrusting sheet) provides a protective barrier and surface on a ship's hull for metal-sensitive species that may otherwise be unable to colonize ships (Visscher 1928; Floerl et al., 2004). This facilitation increases the diversity and invasion risk of the ship fouling vector.

The vast majority of species recorded on ships have only been recorded in one or two studies (Fig. 6), and many of these only on one or two ships. These species are representatives of taxa often associated with ship fouling (barnacles, bivalves, bryozoans and algae) but also from taxa considered unusual in fouling communities and not often associated with invasion risks from ships' hulls. For example, gastropods, chitons, echinoderms, insects, flatworms, and fish, many of which are not known to have non-native distributions, have been sampled on hulls. Most of these instances represent destination port incursions by the novel species and probable failed introductions (in most cases, no data exists that confirms their establishment). Despite their rarity in ship fouling communities, mobile organisms may invade a recipient harbor more readily (by movement) than sessile species when controlling for abundance (i.e. independent of inocula size), and the threat of novel invasions should not be discounted.

A commonality among ships on which atypical ship fouling organisms were recorded was very high accumulation of fouling. Several studies have shown that a small subset of vessels have unusually high diversity and abundance of organisms (e.g. Godwin, 2003; Davidson et al. 2008a). Among 362 vessels for which data were available, 13 had more than 30 species recorded in their fouling communities and decommissioned (obsolete) ships, a replica wooden vessel, and floating docks and rigs were heavily represented among the 13 vessels (Fig. 5 and references therein).

Commercial vessels that had a high diversity of taxa (more than 30 species) generally had an unusual lay-up period prior to sampling that contributed to the accumulation of species (Coutts 2002; Coutts & Taylor, 2004; Drake & Lodge, 2007). In times of economic downturn, the numbers of unemployed or under-used ships within the commercial fleet increases. A recent report showed that slowing demand has resulted in a spike of unemployed containerships amounting to 11% of the global container fleet (The Maritime Executive, 2009). Presumably, these vessels are laid-up until they are hired again, and may transfer an increased abundance and diversity of organisms on their hulls as a result. These high diversity and high abundance vessels are generally considered to carry a high risk of invasions (Godwin, 2005, Drake & Lodge, 2007; Davidson et al. 2008a).

Hull husbandry and voyage effects on biofouling

Antifouling paints have undoubtedly been effective in reducing fouling accumulation on ships and the data show that most ships sampled in the literature were colonized by few species (Fig. 8). It is generally agreed that the per-ship risk of species transfers has decreased through time as antifouling technology has improved (Carlton 1985, Callow & Callow, 2002). Recent studies have pointed out that this trend may not continue, however, because TBT paints that were so effective at preventing biofouling are now banned (Nehring, 2001; Lewis et al., 2004).

While the antifouling paint literature is quite extensive, the ecological macro-trends and overall influence of paint developments on biofouling accumulation over the last century have not been captured quantitatively. Paints with copper biocides appear to be widespread in the commercial fleet and the pollution and invasion impacts of this are being investigated (discussion above; Piola & Johnston, 2008) and we anticipate more research on the effect of foul-release (biocide-free) coatings on species transfers as more ships adopt the technology. One study that included sampling a ship's hull coated with a foul-release coating revealed much higher richness of algae than other vessels using biocidal paints (Mineur et al., 2007).

The available data in our analyses showed positive relationships between age of paint and ship fouling species richness, indicating current antifouling coatings are highly effective initially upon application. The trends of increasing biota over time are not surprising for data that pass through the origin (i.e. no biota at time zero), but there is a striking variability (spread) in the data within and among studies (low 'goodness-of-fit' to trend lines). While performance decays over time, the rate of decay among different coatings and factors that affect performance on operating vessels are not well enough understood to make robust predictions about biofouling magnitude.

Another gap in the ship fouling literature relates to voyage effects on biofouling communities and organisms. The few studies that have measured initial and end-point richness of ship fouling have found increased, decreased and unchanged richness after voyages (Fig. 10). These disparate results did not coincide with voyage distances or durations. The increases in richness because of colonization were a somewhat surprising result of some of these voyages. It is generally assumed that colonization is prevented while vessels are underway and the opposite effect, species removal, is the assumed outcome (Minchin & Gollasch, 2003). It is highly likely that slow moving voyages (and/or those with brief pauses at anchor during the voyage) are the only situations where this is possible, but more data are needed to determine the influence of voyage routes, speeds and durations on fouling organism viability. There are only incidental qualitative data regarding the condition and viability of organisms after transit (e.g. Ruiz et al., 2004; Davidson et al., 2008a), even though this is an important metric of invasion risk assessment. Coutts et al. (2007) have developed a magnetic plate to assess the effects of voyages on biofouling while experimental studies on the effects of voyages (e.g. transits through varying salinities) should produce survivorship and viability data for better modeling and forecasting of the outcomes of species transfers.

Fouling-mediated introductions

Overall, NIS appear to be prevalent on hulls of ships when fouling is present. For example, up to 67% of ships sampled in Germany were found to support at least one species that was non-native to the North Sea coast. While the data are still quite sparse and variable, the presence of NIS on ships arriving at major ports is hardly surprising. Because of the distances regularly traveled by commercial ships nowadays, including round-the-world, interoceanic and transoceanic voyages, it is likely that a proportion of any biota transferred on submerged surfaces will include some species that are potential introductions to ports. This is supported by evaluations of introductions among worldwide locations, where 73% of all 553 NIS at 8 sites can be linked to the fouling vector (Table 2). For some taxa, all of the NIS across the eight sites were considered to have biofouling as a sole or possible vector. The role of biofouling as a transfer mechanism is pivotal for ascidians, for example, where all 27 NIS were considered by multiple authors to be solely vectored by biofouling. Such clear vector association helps to focus management efforts that combat incursions by high impact tunicate invaders, some of which have very serious economic consequences (Coutts 2002; Coutts & Forrest, 2007).

Our literature review indicated that arthropods, annelids, and molluscs were ranked highest in richness among taxa occurring on ships hulls, and this taxonomic distribution mirrors the invasion patterns found in North America (Ruiz et al., 2000), but not in Australia (Hewitt et al., 2004). Hewitt et al. (2004) noted the numerical similarity, broad taxonomic affinity and contribution of biofouling in shaping the NIS communities across southern Hemisphere (Antipodean) locations. When compared to North America, the dominant taxa differ (e.g. bryozoans, cnidaria and ascidians are highest ranked in Australasia) and the fouling vector dominates. In the US, biofouling has not been as dominant a vector of NIS, although intra-regional differences exist (e.g. biofouling ranks highest in LA/Long Beach). Biofouling likely plays a role in the NIS differences among regions because of apparent contrasts in vector strength and patterns of biota recorded on ships in both regions (notably for sponges and ascidians, which were far more prevalent on ships in southern hemisphere studies than US ones).

There was general consistency among sites within regions in the biogeographic patterns of introductions (Table 3). Antipodean locations have had more introductions of species from the NE Atlantic (European coasts) than elsewhere in the world. US Pacific sites have been primarily and consistently invaded by species of transoceanic (Far East Asian) origins. European sites were less clearly invaded by species native to one particular area, but NW Atlantic and North Pacific regions tended to be important donors of European NIS. Of course, the native range of a species may not be the donor region for the invading population, and secondary or stepping-stone invasions have been widely documented (Fofonoff et al., 2003). In fact, secondary invasion is another factor that explains consistency within regions; many species that are introduced primarily from distant regions can be secondarily vectored to nearby sites, including those without major vector hubs (Wasson et al., 2001). Furthermore, the historical pulses of shipping activity and directionality of routes is likely to be similar among sites within regions, such as the European shipping routes to the southern hemisphere in the 1800s (Hewitt et al., 2004). On the US West Coast, introductions from overland vectors from the Atlantic once dominated but were overtaken by Asian species as shipping routes and oyster transplants developed (Ruiz et al., 2000).

Conclusion

The hull fouling vector is a potent transfer mechanism of coastal marine species, particularly the non-dispersal life-stage of many sessile species and several taxa that do not have a planktonic stage of significant duration. Accumulation of biofouling-mediated NIS in different regions of the world indicates that the vector is not just important historically, but has endured through recent years and decades. The record of biofouling studies stretches back at least a century and a half, but there are surprisingly few quantitative studies that have sampled and characterized biofouling communities associated with hulls, especially considering the role the vector has played in altering global biogeography.

Comparisons among the studies that exist are difficult because of temporal, spatial, taxonomic and sampling biases. Differences in methodology, vessel access (dry-dock versus in-water sampling), and limited data presentation (lack of extent and organism condition data), have been a serious impediment to evaluating the effects of major shipping milestones on biofouling transfers over the past century. In particular, the impact of increasing vessel speeds, voyage routes, and the effect of hull husbandry and antifouling paint regulations are not well understood. There have been several insightful studies, however, ranging from detailed analyses of individual ship fouling communities to studies with relatively high numbers of ships sampled ($n > 60$). There has also been a resurgence of ecological research interest in ship fouling over the past decade, prompted by management efforts to evaluate non-ballast shipping vectors. While these recent studies have improved our understanding of the vector process, many critical gaps remain which hinder development of empirically-backed management options for reducing NIS spread in the future.

Potential management options must be grounded in an understanding of the ship fouling vector process. This means ‘pressure points’ need to be identified to interrupt the transfer of species before, during or after transit by influencing organisms during entrainment (attachment), *en route* or at the release stage of the vector process. Most research effort has been expended on antifouling paints as a pre-transit stage (entrainment) management tool, but this effort has occurred independently of ecological assessments of species transfers on ships, as antifouling paints have historically been more concerned with efficient ship operation. Moreover, new generations of antifouling paints are considered less effective than their TBT-based predecessors, requiring further sampling and analysis to evaluate the impact of such coatings on biofouling characteristics and invasion risk.

Perhaps least understood are the effects of transit and post-transit invasion events (organism release). The resistance and resilience of organisms on ships’ hulls to vessel movements and environmental changes undoubtedly varies among functional groups, species, and voyage routes. Yet there are very few data on tolerance of biofouling communities across a range of testable scenarios relevant to recipient ports. Studies to evaluate the condition, viability and invasion potential of biofouling organisms are sorely needed (e.g. Coutts et al., 2007; Davidson et al., in prep).

Unlike ballast-mediated transfers, biofouling organisms are not discharged into the recipient system by ships, but must release themselves, be inadvertently or intentionally knocked-off, or reproduce to infect recipient habitats. While the first and third scenarios are deemed most common for mobile and sessile species, respectively, few studies have examined this formally for fouling communities. Moreover, changes in environmental conditions, a frequent occurrence during transits into port environments, have been reported to induce spawning and other reproductive activity (Minchin & Gollasch, 2003), heightening the risk of invasion. Evaluations of organism reproductive status and cues for reproductive activity may help discern post-arrival management options.

Ideally, future studies will evaluate critical thresholds of propagule supply, and the effects of various voyage conditions and source regions, on likelihood of colonization. Current data indicate a wide variety of species are presently arriving in ports on the hulls of vessels and that this vector is contributing strongly to the increased invasions observed throughout the world. However, the factors that affect the magnitude of hull-fouling and especially the risk of associated invasions are still unresolved. It is these latter aspects that are most needed to develop and implement effective management strategies to reduce invasion risk.

Acknowledgments

We wish to thank Dr Paul Fofonoff for his assistance in assessing species lists for errors and synonymy and providing invaluable historic and biogeographic insight. We also thank A Coutts, O Floerl and LS Godwin for tracking down some elusive references. This study was funded by the California State Lands Commission.

References

Allen FE (1953) Distribution of marine invertebrates by ships. Australian Journal of Marine and Freshwater Research. 4: 307-316.

Anil AC, Chiba K, Okanoto K, Kurokura H (1995) Influence of temperature and salinity on larval development of *Balanus amphitrite*: Implications in fouling ecology. Marine Ecology Progress Series. 118: 159-166.

Arias E, Morales E (1963) Ecolgía del puerto de Barcelona y desarollo de adherencias orgánicas sobre embarcaciones. Inv. Pesq. 24: 139-163.

Bagaveeva EV (1988) Polychaetes in foulings of ships plying coasts in the northwestern part of the sea of Japan. Soviet Journal of Marine Biology. 14:22-26.

Biosecurity New Zealand (2008) Risk Analysis - where are pests coming from, how are they transported and what are our at-risk locations? Website cited February 2009. http://www.biosecurity.govt.nz/biosec/camp-acts/marine-biosec-programme

Bishop MWH (1951) Distribution of barnacles by ships. Nature. 167: 153.

Brock RE, Bailey-Brock JH (1997) Analysis of the invertebrate fauna reported from the hull of the Missouri as a source of possible species introduction to the Hawaiian Islands. Environmental Assessment Co. Report No. 97-11. Honolulu, Hawaii.

Brock R, Bailey-Brock JH, Goody J (1999) A case study of the efficacy of freshwater immersion in controlling introduction of alien marine fouling communities: The *USS Missouri*. Pacific Science. 53: 223-231.

Callow ME (1986) Fouling algae from in-service' ships. Botanica marina. 29: 351-357.

Callow ME, Callow JA (2002) Marine biofouling: a sticky problem. Biologist. 48: 1-5

Carlton JT (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanography and Marine Biology, An Annual Review. 23: 313-371.

Carlton JT (1996) Biological invasions and cryptogenic species. Ecology. 77: 1653-1655.

Carlton JT, Geller JB (1993) Ecological roulette: the global transport of nonindigenous marine organisms. Science. 261: 78-82.

Carlton JT, Hodder J (1995) Biogeography and dispersal of coastal marine organisms: experimental studies on a replica of a 16th-century sailing vessel. Marine Biology. 121: 721-730.

Chilton C (1910) Notes on the dispersal of marine crustacean by means of ships. Transactions of the New Zealand Institute. 43: 131-133.

Cohen, AN (2005) Exotics Guide. San Francisco Estuary Institute, Oakland, CA, www.exoticsguide.org

Coutts ADM (1999) Hull fouling as a modern vector for marine biological invasions: investigation of merchant vessels visiting northern Tasmania. Masters Thesis Australian Maritime College, Launceston, Australia

Coutts ADM (2002) A biosecurity investigation of a barge in the Marlborough Sounds. Cawthron report No. 744. Nelson, New Zealand.

Coutts ADM, Forrest BM (2007) Development and application of tools for incursion response: Lessons learned from the management of the fouling pest *Didemnum vexillum*. Journal of Experimental Marine Biology and Ecology. 342: 154-162.

Coutts ADM, Taylor MD (2004) A preliminary investigation of biosecurity risks associated with biofouling on merchant vessels in New Zealand. New Zealand Journal of Marine and Freshwater Research. 38: 215-229

Coutts ADM, Taylor MD, Hewitt CL (2007) Novel method for assessing the *en route* survivorship of biofouling organisms on various vessel types. Marine Pollution Bulletin. 54:97-110.

Cranfield HJ, Gordon DJ, Willan RC, Marshall BC, Battershill CN, Francis MP, Nelson WA, Glasby CJ, Read GB (1998) Adventive marine species in New Zealand. NIWA Technical Report No. 34. New Zealand.

Darwin CR (1854) A monograph of the sub-class Cirripedia, 2, Balanidae. Ray Society, London.

Davidson IC, Larson K, Schloeder C, Ruiz G (in prep) A preliminary investigation of osmotic stress on a fouling community: voyage effects on ship fouling vectors.

Davidson IC, McCann LD, Fofonoff PW, Sytsma MD, Ruiz GM (2008a) The potential for hull-mediated species transfers by obsolete ships on their final voyages. Diversity and Distributions. 14: 518-529.

Davidson IC, McCann LD, Sytsma MD, Ruiz GM (2008b) Interrupting a mutli-species bioinvasion vector: The efficacy of in-water cleaning for removing biofouling on obsolete vessels. Marine Pollution Bulletin. 56: 1538-1544.

Davidson IC, Ruiz GM, Brown CW, Sytsma M (2007a) Commercial vessel biofouling extent and composition: containerships sampled by diver and ROV survey. Report to the California State Lands Commission. Sacramento, California.

Davidson IC, Ruiz GM, Sytsma MD, Fofonoff P, Mohammad B, McCann L, Zabin C, Altman S (2007b) A post-voyage analysis of hull biofouling on the vessels POINT LOMA and FLORENCE after transit from California to Texas. US Maritime Administration. Washington DC.

Davidson I, Sytsma M, Ruiz G (2006) Preliminary investigations of biofouling of ships' hulls: Non-indigenous species investigations in the Columbia River. U. S. Coast Guard Research & Development Center. Groton, Connecticut.

DeFelice RD (1999) Fouling marine invertebrates on the floating dry dock USS Machinist in Pearl Harbor prior to its move to Apra Harbor, Guam. Contribution No. 1999-013 to the Hawaii Biological Survey. Honolulu, Hawaii.

DeFelice RC, Godwin LS (1999) Records of the marine invertebrates on the hull of USS Missouri on arrival to Pearl Harbor, Oahu, Hawaii. Bishop Museum Occasional Papers. 59: 42-46.

Drake JM, Lodge DM (2007) Hull fouling is a risk factor for intercontinental species exchange in aquatic ecosystems. Aquatic Invasions. 2: 121-131.

Euromonitor International (2009) Global merchant shipping fleet: Euromonitor International from Lloyd's Register/national statistics. Date exported: January, 14th 2009.

Farrapeira CMR, Marrocos de Melo AVO, Barbosa DF, Euzebio da Silva KM (2007) Ship hull fouling in the Port of Recife, Pernambuco. Brazilian Journal of Oceanography. 55: 207-221.

Faubel A, Gollasch S (1996) Cryptostylochus hullensis sp. Nov. (Polycladida, Acotylea, Platyhelminthes): a possible case of transoceanic dispersal on a ship's hull. Helgolander Meeresuntersuchungen. 50: 533-537.

Floerl O, Pool TK, Inglis GJ (2004) Positive interactions between nonindigenous species facilitate transport by human vectors. Ecological Applications. 14:1724-1736.

Fofonoff PW, Ruiz GM, Steves B, Carlton JT (2003) In ships or on ships? Mechanisms of transfer and invasion for nonnative species to the coasts of North America. In: Ruiz GM, Carlton JT (eds) Invasive species: vectors and management strategies. Island Press, Washington DC, pp 152-182.

Foster BA, Willan RC (1979) Foreign barnacles transported to New Zealand on an oil platform. New Zealand Journal of Marine and Freshwater Research. 13: 143-149.

Galil BS (2008) The marine caravan – The Suez Canal and the Erythrean invasion. In: Gollasch S, Galil BS, Cohen AN (eds) Bridging divides: maritime canals as invasion corridors. pp 207-300.

Godwin LS (2003) Hull fouling of maritime vessels as a pathway for marine species invasions to the Hawaiian Islands. Biofouling. 19: 123-131.

Godwin LS, Eldredge LG, Gaut K (2004) The assessment of hull fouling as a mechanism for the introduction and dispersal of marine alien species in the main Hawaiian Islands. Bishop Museum Technical Report, No. 28. Honolulu, Hawaii.

Godwin LS (2005) Hull fouling as a mechanism for marine invasive species introductions. Proceedings of a workshop on current issues and potential management strategies. Honolulu, Hawaii.

Golani D (2004) First record of the muzzled blenny (Osteichthyes: Blenniidae: Omobrnachus punctatus) from the Mediterranean, with remarks on ship-mediated fish introduction. Journal of the Marine Biological Association of the UK. 84: 851-852.

Gollasch S (2002) The importance of ship hull fouling as a vector of species introductions into the North Sea. Biofouling. 18: 105-121.

Gollasch S (2006) Overview on introduced aquatic species in European navigational and adjacent waters. Helgolander Marine Research. 60: 84-89.

Gollasch S, Nehring S (2006) National checklist for aquatic alien species in Germany. Aquatic Invasions. 1: 245-269.

Hewitt CL, Campbell ML, Thresher RE, Martin RB, Boyd S, Cohen BF, Currie DR, Gomon MF, Keough MJ, Lewis JA, Lockett MM, Mays N, MacArthur MA, O'Hara TD, Poore GCB, Ross DJ, Storey MJ, Watson JE, Wilson RS. (2004) Introduced and cryptogenic species in Port Philip Bay, Victoria, Australia. Marine Biology. 144: 183-202.

Hewitt CL, Gollasch S, Minchin D (2009) The vessel as a vector – biofouling, ballast water and sediments. In: Rilov G, Crooks JA (eds) Biological Invasion in marine ecosystems. Springer-Verlag. Berlin, Heidelberg, Germany.

Holmes KL (1969) The historiography of the activities of Francis Drake along the Pacific Coast of North America in 1579. Albion: A quarterly Journal Concerned with British Studies. 1: 30-36.

Huang X, Ni W, Lu H, Cui K (1979) A study of the interrelation between service condition of ships and fouling organisms. Oceanologia et Limnologia Sinica. 10: 82-89.

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology. 46: 10-18.

Karmon Y (1980) Ports around the world. Crown Publishers, Inc. New York.

Kerckhof F, Haelters J, Gollasch S (2007) Alien species in the marine and brackish ecosystem: the situation in Belgian waters. Aquatic Invasions. 2: 243-257.

Lewis PN, Bergstrom DM, Whinam J (2006) Barging in: a temperate marine community travels to the subantarctic. Biological Invasions. 8: 787-795.

Lewis PN, Hewitt CL, Riddle M, McMinn A (2003) Marine introductions in the Southern Ocean: an unrecognized hazard to biodiversity. Marine Pollution Bulletin. 46: 213-223.

Lewis PN, Riddle MJ, Hewitt CL (2004) Management of exogenous threats to Antarctica and the sub-Antarctic Islands: balancing risks from TBT and non-indigenous marine organisms. Marine Pollution Bulletin. 49: 999-1005.

Llanso RJ, Sillett K (2008) Hull biofouling of Suisun Bay reserve fleet vessel Occidental Victory before and after transit from California to Texas. US Maritime Administration. Washington DC.

Lloyd C (1975) Atlas of maritime history. Arco Publishing Co., Inc. New York.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic Invasions: Causes, epidemiology, global consequences, and control. Ecological Applications. 10: 689-710.

Maurer M (1950) Coppered bottoms for the Royal Navy: A factor in the maritime war of 1778-1783. Military Affairs. 14: 57-61.

May RM, (1994) Biological diversity: differences between land and sea. Philosophical Transactions of the Royal Society of London, Biology. 343:105-111.

Minchin D, Gollasch S (2003) Fouling and ships hulls: how changing circumstances and spawning events may result in the spread of exotic species. Biofouling. 19: 111-122.

Minchin D (2007) A checklist of alien and cryptogenic aquatic species in Ireland. Aquatic Invasions. 2: 341-366.

Mineur F, Johnson MP, Maggs CA, Stegenga H (2007) Hull fouling on commercial ships as a vector of macroalgal introduction. Marine Biology. 151: 1299-1307.

Natkiel R, Preston A (1986) Atlas of maritime history. Facts on File Inc. New York.

Nehring S (2001) After the TBT era: alternative antifouling paints and their ecological risks. Senckenbergiana Maritime. 3: 341-351.

NEMESIS (2008) National Exotic Marine and Estuarine Information System. http//invasions.si.edu/nemesis/

Otani M, Oumi T, Uwai S, Hanyuda T, Prabowo RE, Yamaguchi T, Kawai H (2007) Occurrence and diversity of barnacles on international ships visiting Osaka Bay, Japan, and the risk of their introduction. Biofouling. 23: 277-286.

Piola RF, Johnston EL (2006) Differential tolerance to metals among populations of the introduced bryozoan *Bugula neritina*. Marine Biology. 148: 997-1010.

Piola RF, Johnston EL (2008) Pollution reduces native diversity and increases invader dominance in marine hard-substrate communities. Diversity and Distributions. 14: 329-342.

Ritz DA, Foster BA (1968) Comparison of the temperature responses of barnacles from Britain, South Africa, and New Zealand, with special reference to temperature acclimation in *Elminius modestus*. Journal of the Marine Biological Association of the United Kingdom. 48: 545-559.

Ruiz GM, Brown CW, Smith G, Morrison B, Ockrassa D, Nekinaken K (2004) Analysis of biofouling organisms associated with the hulls of containerships arriving to the port of Oakland: A pilot study. In: Ruiz, GM, Smith G. Biological studies of containerships arriving to the Port of Oakland. Oakland, California. pp 138-155.

Ruiz GM, Carlton JT (2003) Invasion Vectors: A conceptual framework for management. In: Ruiz GM, Carlton JT (eds) Invasive species: vectors and management strategies. Island Press, Washington DC, pp 459-504.

Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. Annual Review of Ecology and Systematics. 31: 481-531.

Skerman T (1960) Ship fouling in New Zealand waters: a survey of marine fouling organisms from vessels of the coastal and overseas trade. New Zealand Journal of Science. 3: 620-648.

The Maritime Executive (2009) Unemployed container capacity reaches 1.35 million TEU. Thursday, March 5th, 2009.

Visscher JP (1928) Nature and extent of fouling of ships' bottoms. Bulletin Bureau of Fisheries. 43: 193-252.

Visscher JP (1938) Some recent studies on barnacles. Biological Bulletin. 75: 335-379.

Ward C (2006) Boat-building and its social context in early Egypt: interpretations from the First Dynasty boat-grave cemetery at Abydos. Antiquity. 80: 118-129.

Wasson K, Zabin CJ, Bedinger L, Diaz MC, Pearse JS (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. Biological Conservation. 102: 143-153.

Zullo VA (1966) Thoracic cirripedia from the continental shelf of South Carolina USA. Crustaceana. 11: 229-244.

Zvyagintsev AY (2003) Introduction of species into the Northwestern Sea of Japan and the problem of marine fouling. Russian Journal of Marine Biology. 29: S10-S21.